

Climate change, tourism and historical grazing influence the distribution of *Carex lachenalii* Schkuhr – A rare arctic-alpine species in the Tatra Mts

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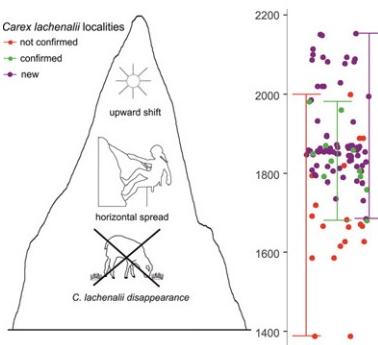
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HIGHLIGHTS

- We assessed niche shift of a model arctic-alpine species.
- Vegetation pattern shows competition – mediated retreat from lower elevations.
- Climate warming allowed colonization of higher elevations, lacking in competitors.
- Modern habitat changes both threats and promotes rare mountain plant species.

GRAPHICAL ABSTRACT



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ABSTRACT

Mountain vegetation is highly specialized to harsh climatic conditions and therefore is sensitive to any change in environment. The rarest and most vulnerable plants occurring in alpine regions are expected to respond rapidly to environmental changes. An example of such a species is *Carex lachenalii* subsp. *lachenalii* Schkuhr, which occurs in Poland on only a few isolated sites in the Tatra Mts. The aim of this study was to assess changes in distribution of *C. lachenalii* in the Tatra Mts over the past 50–150 years and the effects of climate change, tourism and historical grazing on the ecological niche of *C. lachenalii*. We focused on changes in the importance of functional diversity components in shaping plant species composition. Over the past 50–150 years, the elevation of the average distribution of *C. lachenalii* shifted about 178 m upward alongside a significant prolongation of the vegetative season by approximately 20 days in the last 50–60 years. Species composition of plots without *C. lachenalii* was characterized by competition between plants, whereas on plots with *C. lachenalii* habitat filtering was the most important component. Our results suggest that climate change was the main factor driving upward shift of *C. lachenalii*. Moderate trampling enhanced horizontal spread of this plant, whereas cessation of grazing caused decline of *C. lachenalii*. The three environmental factors studied that determined shifts in distribution of *C. lachenalii* may also contribute to changes in distribution of other rare mountain plant species causing changes in ecosystem functioning.

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1. Introduction

Mountain ranges are hotspots of plant species diversity, with concentrations of endemic and sub-endemic species, glacial relicts, and species at the edge of their geographical range (Körner, 2003; Nagy and Grabherr, 2009; Erschbamer et al., 2011). As these plants often are highly specialized, they may respond relatively fast to shifts in environment (Theurillat and Guisan, 2001; Klug et al., 2002; Grabherr, 2003; Erschbamer et al., 2011; Jägerbrand and Alatalo, 2015). The most important drivers influencing dynamics of alpine flora and vegetation are climate change (e.g. Evangelista et al., 2016), tourism (e.g. Jägerbrand and Alatalo, 2015) and changes in land-use (e.g. Sheil, 2016).

Effects of recent climate change on alpine flora and vegetation have been explored over broad latitudinal and elevational gradients across the world (e.g. Lenoir et al., 2008; Chen et al., 2011; Engler et al., 2011; Lenoir and Svenning, 2015) and Europe, including the Alps, Scandes, Pyrenees and Apennines (e.g. Klanderud and Birks, 2003; Sanz-Elorza et al., 2003; Vittoz et al., 2008; Evangelista et al., 2016). Climate warming drives an upward migration of species (e.g. Wilson and Nilsson, 2009; Grytnes et al., 2014), increases species richness on mountain summits (e.g. Pauli et al., 2007; Odland et al., 2010), increases primary production (e.g. Spasojevic et al., 2013) and causes thermophilization of mountain floras (e.g. Grabherr et al., 2010; Matteodo et al., 2013; Evangelista et al., 2016). As the specific interactions between species change in a warmer climate, plant specialists are often replaced by generalists and the homogenization of plant communities takes place (Olden et al., 2004; Britton et al., 2009; Ross et al., 2012). The magnitude of these changes depends mainly on species traits connected with dispersal ability and resistance to unfavorable environmental conditions, as well as inter- and intra-specific competition (e.g. Sandvik et al., 2004; Lenoir et al., 2008; Parolo and Rossi, 2008).

Aside from climate change, tourism is often listed as one of the important factors driving changes in plant species composition of high-elevation areas (e.g. Grabherr et al., 2010; Whinam and Chilcott, 1999; Klug et al., 2002; Crisfield et al., 2012). Trampling associated with tourism increases soil compaction, erosion and changes soil humidity (Pickering et al., 2003; Jägerbrand and Alatalo, 2015). As a result, decreases in species richness, plant frequency, cover and biomass are found on disturbed areas in comparison with undisturbed surroundings (Whinam and Chilcott, 1999; Klug et al., 2002; Gremmen et al., 2003). Intensive trampling also leads to reduction of stem length, total leaf area, flower density and seed size and production (e.g. Cole and Monz, 2002; Janyszek et al., 2008; Crisfield et al., 2012; Jagodziński et al., 2017). The trampling-resistant species are tufted grasses and sedges with a high number of short stems close to the soil surface, relatively small seeds and high ability of vegetative dispersion, as well as low competitive abilities (Grabherr et al., 2010; Klug et al., 2002; Janyszek et al., 2007; Bernhardt-Römermann et al., 2011; Ballantyne et al., 2014).

Another important factor is land-use change, including cessation of grazing, which in mountains leads to an upward shift of the treeline (e.g. Gehrig-Fasel et al., 2007) and results in a decrease in the number and heterogeneity of local microhabitats on high-elevation meadows, mainly due to increasing competition between species (e.g. Amezaga et al., 2004; Baur et al., 2006; Sheil, 2016). Thus, in abandoned meadows, the proportion of light demanding species decreases and they are gradually replaced by more shade-tolerant and productive plants (Witkowska-Żuk and Ciurzycki, 2000; Başnou et al., 2009) leading to decrease in species richness (e.g. Dupré and Diekmann, 2001; Baur et al., 2006).

Alpine snowbed plant communities are usually dominated by glacial relicts. These are an extremely specialized type of vegetation, assumed to be particularly sensitive to environmental shifts (e.g. Grabherr et al., 2010; Sandvik et al., 2004; Björk and Molau, 2007; Sandvik and Odland, 2014). Therefore, focusing on populations of relict species may be a suitable way to understand changes in vegetation diversity of high-elevation mountain areas (Holzinger et al., 2009). A model species

for this guild is *Carex lachenalii* Schkuhr – a small tufted perennial sedge with short stolons, typically occurring in low-productivity wet snowbeds and granite grassland vegetation (Mirek and Piękos-Mirkowa, 1992). According to the Global Biodiversity Information Facility (<http://gbif.org>) and Euro + Med (2006), *C. lachenalii* is divided into two subspecies: *C. lachenalii* subsp. *lachenalii* Schkuhr is common in many mountain regions of Asia (e.g. Kolyma Mts, North America (e.g. Alaska), Northern Europe (e.g. the Scandes), as well as Central and Southern Europe (e.g. the Pyrenees and the Carpathians). *Carex lachenalii* subsp. *parkeri* (Petrie) Toivonen is endemic to New Zealand (Toivonen, 1979) and often considered as a separate species *C. parkeri* Petrie (Petrie, 1881; Toivonen, 1979; Govaerts and Simpson, 2007) despite relatively low genetic difference between the two taxa (Volland et al., 2006). According to the IUCN Red List of Threatened Species (2017), *C. lachenalii* is considered a least concern species, whereas in Central and Southern Europe the species is rare and endangered (e.g. Moser et al., 2002; Villar, 2004; Romand-Monnier, 2013; Turis et al., 2014), including in the Tatra Mts, where it occurs only in a few isolated sites and is considered as a vulnerable species (Mirek and Piękos-Mirkowa, 2014). Most of the historical records in the Tatra Mts have not been re-confirmed since the 1970s and date back to the years 1872–1969 (Supplementary material 1).

The goals of this research were to assess: changes in distribution of *C. lachenalii* in the Tatra Mts over the past 50–150 years and the effects of climate change, recent tourism and historical grazing on the ecological niche of *C. lachenalii*.

We hypothesized that climate change, expressed as a decrease in snow cover duration linked with prolongation of the growing season, may drive an upward elevational shift of *C. lachenalii* (e.g. Lenoir and Svenning, 2015). As vegetation at high elevations is highly specialized to harsh climatic conditions (Theurillat and Guisan, 2001), we assumed that the importance of habitat filtering, expressed by low values of functional diversity indices – functional richness (FRic) and functional dispersion (FDis) – will increase with increasing elevation, mainly by promoting specialized species (Laliberté and Legendre, 2010). Thus we predicted that *C. lachenalii*, as a snowbed-specialist species, may be not able to compete with generalists, as long as environmental conditions are not particularly extreme. This may be expressed as a higher role of habitat filtering in shaping plant species composition of plots with *C. lachenalii* at the highest elevations, in comparison to sites without *C. lachenalii*. We further assumed that the probability of *C. lachenalii* occurrence would increase along with increasing elevation above sea level.

As tourism promotes mainly trampling-resistant tufted graminoids (e.g. Jägerbrand and Alatalo, 2015), we assumed that the densities of *C. lachenalii* would be higher on plots located closer to tourist trails. Thus, we hypothesized that tourism may drive a horizontal spread of this species.

As an effect of cessation of grazing, the importance of competition between plants increases (e.g. Onipchenko et al., 2009). *C. lachenalii* is a plant occurring mostly in highly specialized vegetation (snowbeds), thus we hypothesized that this species has low competitive abilities. Therefore it may decline on sites characterized by high competition, and we predicted that species composition of plots without *C. lachenalii* will be characterized by high values of functional divergence (FDiv) and functional evenness (FEve), indicating a greater role of competition in comparison to plots with *C. lachenalii*. To observe this pattern we used a set of ecological indicator values (Zarzycki et al., 2002): light EIV (EIV-L), temperature EIV (EIV-T), moisture EIV-F and nitrogen (EIV-N).

2. Materials and methods

2.1. Area of study

Most of the area of the Tatra Mts is composed of granitic and metamorphic rocks, formed during the Hercynian orogeny. The alpine vegetation of this area shifts from dwarf pine communities (1550–1850 m a.s.l.), through low-productive alpine acidophilous grasslands (1850–

2300 m a.s.l.) to bare rocks with low cover of vascular plants in the subnival zone of the highest elevations (Mirek and Piękoś-Mirkowa, 1992).

The climate of the Tatra Mts, as in other European mountain regions, is characterized by low annual mean air temperature (-0.7°C) and high precipitation (about 1800 mm per year; Limanówka et al., 2008). Over the past 50–60 years the climate in the Tatra Mts has changed significantly: according to the climatic data from Łomnica Meteorological Observatory (High Tatra Mts; 2634 m a.s.l.), mean annual temperature and rain precipitation increased ($R^2 = 0.46, p < 0.001$ and $R^2 = 0.49, p < 0.001$, respectively), whereas the number of days with snow decreased ($R^2 = 0.17, p < 0.01$). In effect the vegetative season, understood as the number of days with mean daily temperature above 5°C , expanded significantly from 85 to 105 days on Kasprowy Wierch (Western Tatra Mts; 1987 m a.s.l.) and from 181 to 209 days in Zakopane (855 m a.s.l.) during the period 1960–2016 (Supplementary material 2).

Over the last century, the Tatra Mts attracted the attention of many tourists, particularly those interested in recreational hiking. It is estimated that since the 1990s this area has been visited each year by about 2.5 million people (Mirek, 1996). Due to the numerous inaccessible areas such as rock walls, shelves and steep-sloped summits, the Tatra Mts are also widely explored by mountain climbers. According to Jodłowski (2003), the most attractive areas are located in the High Tatra Mts (mainly Morskie Oko Lake Region) which are visited by approximately 1600 climbers annually.

The period of increase in tourist exploration overlapped with the cessation of grazing. Grazing started in the Tatra Mts range in the 15th century and even in the High Tatra Mts it dates to the 17th century (Śmiałowska, 1962). The intensity of sheep grazing increased over the centuries and at its peak the number of sheep and cattle grazed was approximately three million. Sheep herding in the Tatra Mts covered all accessible areas, i.e. those with relatively low steepness and those with considerable shares of exposed rock formations or shelves. The primary production of high-elevation pastures is lower in comparison to those located at lower elevations, where grazing intensity was the highest (Mirek, 1996). Grazing disappeared almost completely over the years 1963–1968 due to the establishment of the Tatra National Park in 1955 and following changes in land ownership structure (Balcerkiewicz, 1984). After the 1970s sheep herding was practiced only on partly-protected areas of the National Park devoted to so-called cultural sheep herding, aimed at the maintenance of species rich mountain meadows (Mirek, 1996).

2.2. Study design

The study was carried out in August 2016 across the High and Western Tatra Mts over an elevation gradient 1400–2200 m a.s.l. (Fig. 1). We revisited all 27 known historical localities of *Carex lachenalii* from the years 1872–1969 (Supplementary material 1), when intensive grazing was still in place (Balcerkiewicz, 1984). Almost all study sites were located in the High Tatra Mts, except for two located in the Western Tatra Mts. The elevation of the historical locality was missing in 16 cases. Therefore, we estimated the approximate elevations of these sites using historical descriptions, including information contained in the name of specific places in the mountains (e.g. mountain lake, scree, valley, couloir), in whose proximity *C. lachenalii* was recorded. We also investigated all accessible areas over the whole elevation gradient with the presence of habitats that were potentially suitable for this species (granite grasslands and snowbeds with low cover of vascular plants). For all confirmed localities of *C. lachenalii* we recorded: elevation above sea level; abundance of all vascular plant species accompanying *C. lachenalii*, using the seven-level alpha-numerical scale of Braun-Blanquet (1913); density of *C. lachenalii* expressed as the number of shoots per 100 m^2 and mean distance of each individual tuft of *C. lachenalii* to the nearest tourist trail, which we used as a proxy of the intensity of trampling (in meters; Supplementary material 3). We defined an individual tuft as “a group of

ramets growing together at high density and connected by stolons”. This assumption was made with a caution that the distance to the next group was bigger than 5 cm and there was no vegetative connection existing between the groups.

In order to explore specific interactions between *C. lachenalii* and other plant components of the snowbeds and acidophilous grasslands, we compared our vegetation data (96 plots at elevations between 1682 and 2153 m a.s.l.; Supplementary material 4) with data from 47 plots on the same plant communities scattered at elevations between 1380 and 2170 m a.s.l., collected in July and August 2015 (Czortek et al., 2017, in press) in the Morskie Oko Lake Region, where *C. lachenalii* could potentially occur. The Czortek et al. (2017, in press) study used relatively large plot sizes which varied from 5 to 3000 m^2 , whereas the present study was carried out within 100 m^2 plots. Therefore, to check whether a plot size effect could influence our results, we compared plot sizes with plot species richness in the Czortek et al. data from the Morskie Oko Region. This was done both for snowbed and acidophilous grassland communities separately. In both cases the relationship between plot size and plot species richness was insignificant ($p > 0.05$; Supplementary material 5). Therefore, we are confident that our results have not been affected by a plot size effect.

2.3. Species and plant community characteristics

To characterize the plant species ecological requirements for light (EIV-L), temperature (EIV-T), moisture (EIV-F), nitrogen (soil nutritional requirement indicator corresponding to plant productivity, EIV-N) and soil reaction (EIV-R) we used the Zarzycki et al. (2002) modification of the Ellenberg et al. (1992) ecological indicator scale. As ecological indicator values reflect the realized niche – the outcome of a complex of environmental factors that are changing over time (e.g. Smart and Scott, 2009) – we compiled the species from all datasets and explored relationships between EIVs. This was done using Pearson's correlation method with a maximum level of significance set at $p = 0.05$. We found that EIV-T and EIV-L, as well as EIV-L and EIV-N, were strongly negatively correlated (Pearson's $r = -0.60$ and $r = -0.45$, respectively; $p < 0.001$ in both cases). We observed a strong positive correlation between EIV-T and EIV-N (Pearson's $r = 0.50$; $p < 0.001$), and in parallel a relatively strong relationship between EIV-N and EIV-R (Pearson's $r = 0.45$; $p < 0.001$). Therefore, as these EIVs were strongly correlated, changes in community-weighted mean values (CWM) of ecological indicator values were considered jointly (Supplementary material 6).

We also compiled information about plant species functional traits: leaf mass, total dry matter content and broad characterization of growth form (rosette-like versus erect stems), specific leaf area, canopy height, seed mass and their number per shoot and self-sterility (Table 1). All traits were provided by the LEDA database (Kleyer et al., 2008), except for life strategy which we found in the BiolFlor database (Klotz et al., 2002).

For each plant community we calculated CWM of ecological indicator values and components of functional diversity: functional richness (FRic), evenness (FEve), divergence (FDiv) and dispersion (FDis), following Mason et al. (2005). These parameters describe distribution of species' functional traits within the plant community trait hypervolume (Laliberté and Legendre, 2010) and explain the significance of competition as well as environmental filtering in forming specific plant community species composition. The prevalence of competition is indicated by high FDiv and FEve and the prevalence of habitat filtering by low FRic and FDis (Kotowski et al., 2010; Laliberté and Legendre, 2010; Hedberg et al., 2014, but see Kraft et al., 2015). For these calculations we used the *FD::dbFD()* function (Laliberté et al., 2014). We also calculated species richness and diversity, expressed by Shannon's index using the *vegan::diversity()* function (Oksanen et al., 2016).

The nomenclature of species followed Euro + Med (2006). All species of the genus *Alchemilla* L. were excluded from the analyses due to species identification difficulties and taxonomical uncertainties resulting from

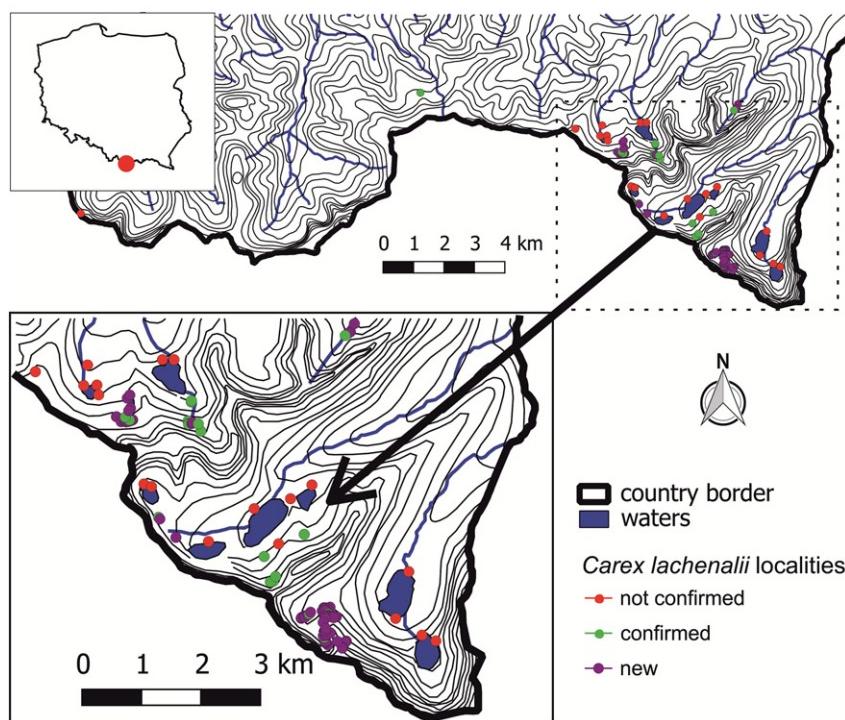


Fig. 1. Distribution of *Carex lachenalii* in the Tatra Mts.

the presence of numerous forms (e.g. Hayırlıoğlu-Ayaz and Beyazoğlu, 2000).

2.4. Data analyses

To find out whether there was an elevational range shift of *C. lachenalii* the elevation of each recent plot was compared with the elevation of historical records using the Student's *t*-test. To show relationships between traits of plant communities containing and not containing *C. lachenalii* we used ordination techniques. Due to long gradient (>3 SD units) reported by preliminary Detrended Correspondence Analysis (DCA) we decided to use DCA in analysis. To perform DCA we used the *vegan::decorana()* function (Oksanen et al., 2016). We also checked importance of CWMs, functional diversity components, species richness and diversity, as well as elevation and the distance from the nearest tourist trail as vectors passively fitted to DCA results, using *vegan::envfit()* (Oksanen et al., 2016).

Table 1

Parameters of environmental variables passively fitted to the DCA ordination results. Determination coefficients R^2 and *p*-values were estimated using permutation tests with 999 iterations. Abbreviations: EIV—ecological indicator value (Zarzycki et al., 2002). Stars in the last column denote level of statistical significance: * $p < 0.01$; n.s. – not significant.

Parameter	Abbreviation	DCA1	DCA2	R^2
Species richness	Rich	0.99801	−0.06303	0.5605*
Elevation	Elev	−0.67263	0.73998	0.4387*
Functional diversity indices:				
Functional richness	FRic	0.99504	0.09952	0.1286*
Functional dispersion	FDis	0.61716	−0.78684	0.4373*
Functional divergence	FDiv	0.41039	0.91191	0.1677*
Functional evenness	FEve	0.99385	0.11072	0.0212 n.s.
Ecological indicator values:				
Light EIV	EIV-L	−0.74293	0.66937	0.7189*
Moisture EIV	EIV-F	0.55186	0.83394	0.3765*
Soil reaction EIV	EIV-R	0.59640	0.80270	0.8200*
Fertility EIV	EIV-N	0.95045	0.31089	0.7854*
Temperature EIV	EIV-T	0.51444	−0.85752	0.6872*

To reveal the relationships between *C. lachenalii* presence/absence and environmental parameters we used logistic regression implemented in generalized linear models (GLM), using the *stats::glm()* function with a binomial distribution of response variable. For assessment of relationships between FDis and elevation, as well as between *C. lachenalii* density and distance to the nearest trail we used simple linear regression. We inspected model diagnostic plots for maintaining homoscedasticity of residuals. We also checked outliers and as they did not influence trajectories of models, we did not exclude them. Before GLMs we pre-processed all variables by scaling, centring and Yeo-Johnson power transformations (Yeo and Johnson, 2000) using the *caret::preProcess()* function (Kuhn, 2008).

All analyses were performed using R software (R Core Team, 2016). Due to lack of replications, we excluded from the analyses one untypical *C. lachenalii* locality in a mylonite grassland community (plot no. 63, Supplementary material 4).

3. Results

Within 27 revisited historical localities, *C. lachenalii* was confirmed on 11 (Fig. 2). Over the past 50–150 years the average elevation of *C. lachenalii* occurrences shifted about 178 m upward. We discovered 84 new sites for the species, mainly at elevations between 1800 and 1900 m a.s.l. (50 records). A relatively high number of new localities was recorded at elevations above 2000 m a.s.l., including the highest one in the Tatra Mts (2153 m a.s.l.). Most of the historical records of *C. lachenalii* that were not re-confirmed were from elevations below 1700 m a.s.l.

There was high dissimilarity between species composition of snowbed and granite grassland vegetation according to the DCA ordination (Fig. 3). However, we also observed a partial continuum in the vegetation types surveyed: some of the symbols representing snowbeds and granite grasslands were overlapping on the middle and the left side of the DCA plot.

The main factors determining plant species composition of snowbed communities with *C. lachenalii* were relatively high values of EIV-L that positively corresponded with a vector representing higher elevations

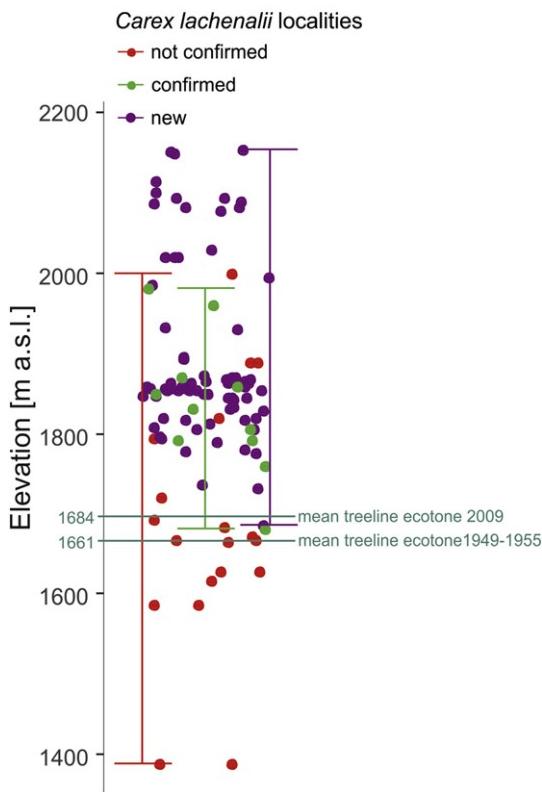


Fig. 2. Elevational upward shift of *Carex lachenalii* after 50–150 years.

above sea level (Elev; Table 1; Fig. 3). These two factors were negatively correlated with FDis and EIV-T, indicating that lower values of FDis and EIV-T were important factors that described the diversity of such plant communities. The vector representing FDiv was positively associated with EIV-F, showing that high values of these factors determined the diversity of snowbeds with a presence of *C. lachenalii*, as well as plots

where this sedge could potentially occur. Lower values of FDiv, EIV-F and EIV-R described well the diversity of granite grasslands (bottom-left side of DCA plot; Fig. 3). Higher values of FDis and EIV-T, which were associated positively with each other and described the diversity of lower-elevation granite grassland communities without *C. lachenalii* (bottom-right side of DCA plot; Fig. 3). In the same group of plots that were located on the right side of the DCA plot, equally important were vectors representing higher values of EIV-N and EIV-R, species richness and FRic. We found that these four factors were positively correlated, indicating the strongest relationship between EIV-N and species richness (Rich).

The probability of *C. lachenalii* occurrence significantly decreased ($p < 0.01$) with increasing elevation of snowbeds from 0.75 at 1900 m a.s.l. to 0.37 at the highest elevations, whereas on granite grasslands it increased from 0.37 at lowest elevations to 0.62 at 2200 m a.s.l. (Fig. 4a). Probability of occurrence of *C. lachenalii* decreased with increasing plot species richness ($p < 0.001$), regardless of type of vegetation (Fig. 4b). Within plots representing snowbed communities, as well as acidophilous grasslands, the maximum number of species indicating the probability of occurrence of *C. lachenalii* equal to zero was about 50 species per plot. The highest probabilities (0.8–0.9) we observed at the lowest numbers of species per plot (10–20 species). Elevation was negatively correlated with FDis ($p < 0.001$; $R^2 = 0.31$; Fig. 4c). In both types of vegetation, and in patches with and without *C. lachenalii*, FDis significantly decreased with increasing elevation. In granite grasslands FDis decreased from about 0.17 at the lowest elevations to about 0.13 at elevations close to 2200 m a.s.l., whereas on snowbeds it decreased from 0.15 at 1650 m a.s.l. to 0.13 at the highest elevations.

The density of *C. lachenalii* was negatively correlated with distance from the nearest tourist trail ($p < 0.001$; $R^2 = 0.39$; Fig. 4d). In granite grasslands, the highest densities of *C. lachenalii* were found at tourist trails and in their direct vicinity (to 0.5 m from the trail). A similar trend was found for snowbeds indicating the highest densities of this plant at distances 0.5–10 m from the nearest path.

4. Discussion

4.1. Competition vs. species composition

We found that the species composition of plots with and without *C. lachenalii* differed considerably, independent of vegetation type studied. Species composition of plots without *C. lachenalii* was best described by competition between plants, whereas on plots with *C. lachenalii* habitat filtering was the most important component characterizing the species composition. We also found that along with increasing elevation, the importance of competition decreased, but its role in describing species composition was shaped by different environmental drivers at different elevations.

4.2. Upward shift of *C. lachenalii*

The current average elevation of population shifted upward by approximately 178 m in comparison with historical data. The highest recent records of *C. lachenalii* in the Tatra Mts (above 2000 m a.s.l.) are on areas not favourable for grazing due to low productivity, numerous steep bare rocks, rock walls and shelves. Thus, we are confident that the upward colonization revealed was independent of grazing. Similar tendencies were found for many plant species, indicating upward shifts strongly linked to recent global temperature increase (e.g. Chen et al., 2011; Felde et al., 2012). An elevational shift of *C. lachenalii* may be explained by prolongation of growth season observed in the Tatra Mts during the last 54 years of climate monitoring. The high duration of snow cover and frequency of negative temperatures during the year are the main factors that shape abiotic conditions in alpine areas (Hiller et al., 2005). The duration and thickness of snow cover determine relatively short growing seasons, population dynamics and length

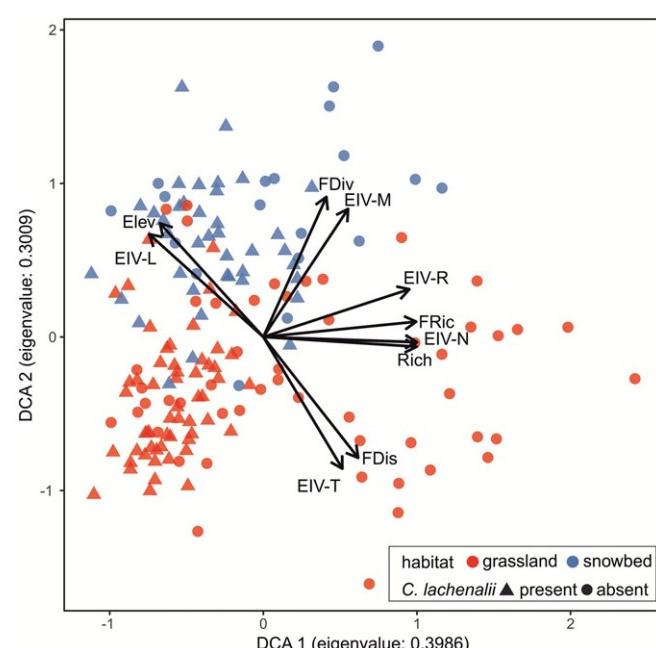


Fig. 3. DCA ordination performed on plots without ($n = 70$) and with *C. lachenalii* ($n = 95$) with passively fitted vegetation traits (black arrows): FDiv – functional divergence, FRic – functional richness, FDis – functional dispersion, Rich – species richness, Elev – elevation; ecological indicator values: EIV-L – light, EIV-T – temperature, EIV-M – moisture, EIV-N – nitrogen, EIV-R – soil reaction.

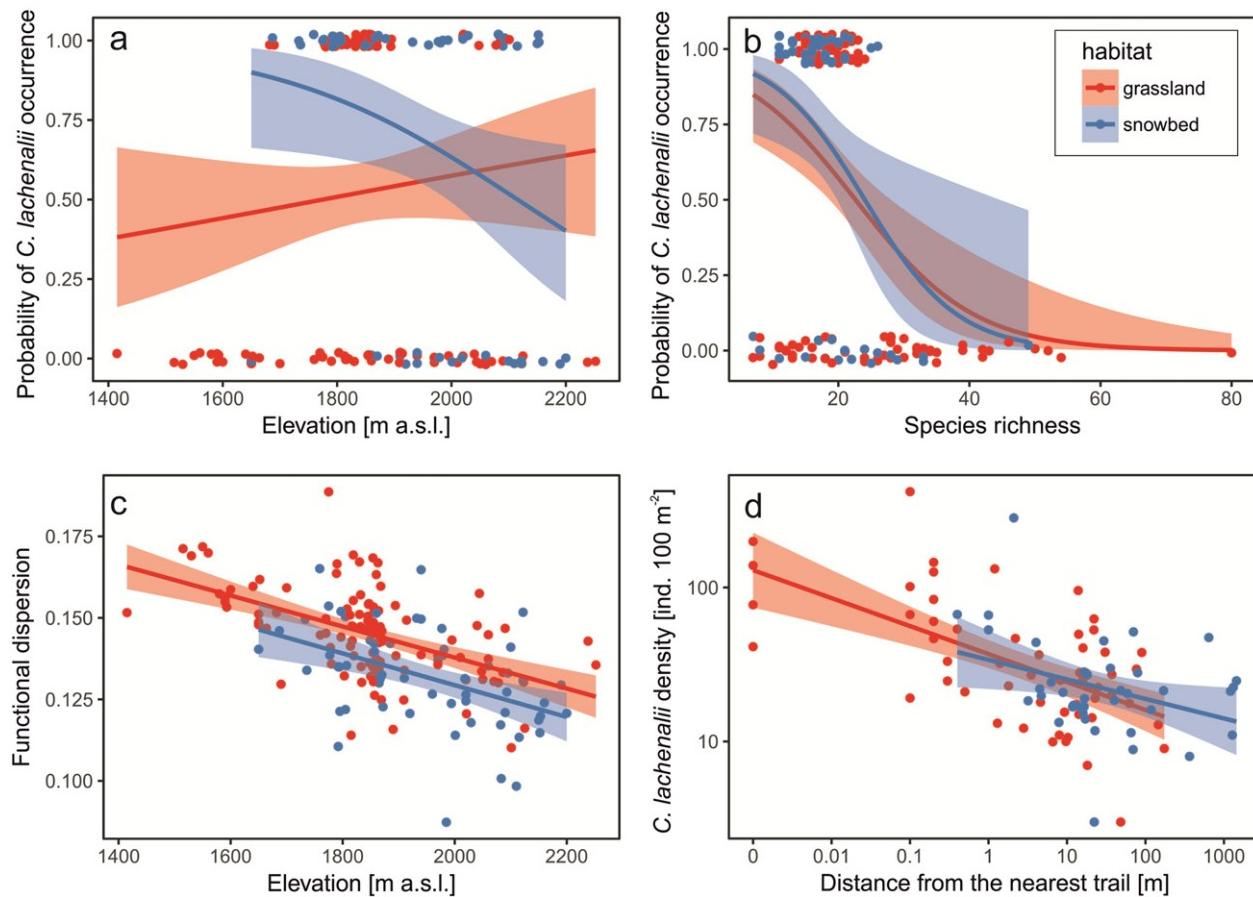


Fig. 4. Relationships between: elevation and probability of *C. lachenalii* occurrence (a) and functional dispersion (b), probability of *C. lachenalii* occurrence and species richness (c), and relationship between *C. lachenalii* density and distance from the nearest trail (d). Note log-transformation of axes in (d).

of time available for generative reproduction (e.g. Carlsson and Callaghan, 1994). With the earlier snowmelt, growing season length has increased but soil water content decreased due to increased soil evaporation. In effect, snowbed communities have been colonized by species that tolerate drier conditions (e.g. Callaghan et al., 2011; Daniëls and de Molenaar, 2011; Sandvik and Odland, 2014). In a warmer climate *C. lachenalii*, which prefers relatively wet and cold habitat conditions, may successfully colonize snowbeds, replacing (or co-occurring with) the wet demanding grasses *Poa laxa* and *P. granitica*. An illustration of this pattern may be the low FDIs values observed on most of those snowbeds with *C. lachenalii* in comparison with plots where this plant was not found. Low FDIs, which decreased significantly along with increasing elevation, indicated high importance of habitat filtering, preventing establishment of many functional plant types and promoting only specialized species (Laliberté and Legendre, 2010) adapted to the harsh climatic conditions, typical for the sites located at the highest elevations (Theurillat and Guisan, 2001).

The probability of occurrence of *C. lachenalii* decreased significantly on snowbeds with increasing elevation. However, the probability of recording this plant at the highest elevations was still relatively high (0.37), which showed that *C. lachenalii* may potentially colonize the highest snowbed communities, those located at elevations above 2200 m a.s.l. and dominated by highly wet-demanding bryophytes (e.g. Mucina et al., 2016). This is in line with other findings (e.g. Molaw and Larsson, 2000; Welling and Laine, 2000; Tevendale, 2006), which showed high colonization abilities of *C. lachenalii*. Similar patterns were observed for other species which in Central Europe are at the edge of their geographical range, e.g. *C. atrofusca* and *C. bigelowii* in the Alps and the High Tatras, as well as *C. nigra* in the Mediterranean Basin and Western Russia (Schönswetter et al., 2006; Schönswetter et al., 2008;

Jiménez-Mejías et al., 2012). In contrast, on granite grasslands the probability of occurrence of *C. lachenalii* increased significantly with increasing elevation. This tendency could be explained on the one hand by the fact that in terms of decreased snow cover duration, some dwarf shrub species (*Vaccinium* spp. and *Empetrum* spp.) may become more exposed to wind and frost, which could limit their growth and cover (e.g. Grytnes et al., 2014) and decrease competition. As an effect, new microhabitats would become available for colonization by *C. lachenalii* (e.g. Matthews, 1992) and similar species. On the other hand, relatively low probabilities of *C. lachenalii* occurrence at lower elevations may suggest climate-driven colonization of more competitive plants from lower elevations (e.g. Britton et al., 2009; Odland et al., 2010; Ross et al., 2012), indicating the low competitive abilities of *C. lachenalii*.

4.3. Horizontal spread of *C. lachenalii*

Most of the new localities of *C. lachenalii* were at elevations between 1800 and 1900 m a.s.l., mainly at the foot of the Mnich summit (2068 m a.s.l.), the most popular site for extreme climbing in the whole Tatra Mts range (Jodłowski, 2003). Areas located in the closest neighbourhood of the Mnich, mainly the Valley Za Mnichem (1830–1870 m a.s.l.), are the starting points and resting places for climbers. These areas are covered by a dense net of paths with a moderate trampling intensity, which promote trampling-resistant tufted graminoids rather than intolerant herbs, mainly due to soil compaction and erosion (Bernhardt-Römermann et al., 2011; Ballantyne et al., 2014; Jägerbrand and Alatalo, 2015). *Carex lachenalii* is one of those trampling-resistant plants: its density, expressed as the number of individuals per 100 m², was highest right beside the paths and decreased significantly with distance from tourist trails.

Moderate trampling creates new microhabitats causing higher physical isolation between individuals. Therefore, only specialized species may develop on such disturbed sites. *Carex lachenalii* colonized trampling-disturbed sites, taking advantage of anthropogenic seed and vegetative propagule dispersal on climbers' shoes, clothing and equipment (e.g. Grabherr, 2003; Klug et al., 2002; Whinam et al., 2005).

4.4. Decline in historically grazed areas

We did not re-confirm *C. lachenalii* on most of historical locations that were below 1700 m a.s.l. These areas had been intensively grazed by sheep and cattle until the end of the 1960s (Balcerkiewicz, 1984). The occurrence of *C. lachenalii* on such areas was possible due to high grazing intensities (Mirek and Piękoś-Mirkowa, 2014), which decreased role of inter-specific competition. As sheep and cattle grazing ceased on these locations, shrubs, tall herbs and grasses with high competitive potential became more common, and thus due to its low competitive abilities *C. lachenalii* was replaced by them (e.g. Amezaga et al., 2004).

We found that on the plots where *C. lachenalii* was absent, the main factors describing the diversity were high FDiv, FRic and FDis, indicating the decreasing role of habitat filtering and increasing competition between species. Our results are in line with other findings showing high resilience of *C. lachenalii* to grazing (Molaw and Larsson, 2000; Welling and Laine, 2000; Tevendale, 2006). Similarly, increasing competition between species is one of the drivers describing shifts in diversity on areas where grazing ceased, mainly by a decrease in the number of local microhabitats and following homogenisation of environment (e.g. Amezaga et al., 2004; Baur et al., 2006; Sheil, 2016). A significant negative relationship between species richness and probability of occurrence of *C. lachenalii* may be a supporting explanation of the role of competition between species in shaping plant species composition on non-grazed areas.

The diversity of granite grasslands without *C. lachenalii* (which had high values of FDis) was characterized by a relatively high proportion of warm-demanding and shade-tolerant species (high EIV-T and low EIV-L, respectively). Plant species ecological requirements on plots associated with higher values of FRic were described by higher EIV-N and EIV-R (middle-right side of DCA plot; Fig. 3). The increasing competition and proportion of more nitrogen-demanding species and decreasing number of light-demanding species after cessation of grazing was reported by Witkowska-Żuk and Ciurzycki (2000) and Başnou et al. (2009). Owing to establishment of wind- and frost-sheltered microhabitats under the canopy of more productive nitrophilous species (e.g. Hiller et al., 2005), the alpine flora may become more thermophilous and at the same time characterized by a higher proportion of more shade-tolerant species.

4.5. Combined effect of climate change, historical grazing and tourism

Effect of climate change may interact with changes in grazing regimes and tourism (e.g. Klanderud and Birks, 2003; Becker et al., 2007; Frei et al., 2010; Felde et al., 2012; Speed et al., 2012). Thus, observed horizontal spread of *C. lachenalii* at lower elevations, and its disappearance at the lowest elevations, may be an effect of combination of the three factors studied. As we could not find a clear signal from climate change on the distribution changes of *C. lachenalii* on lower-elevation snowbeds and granite grasslands, the observed compositional shifts could be explained by the masking effect of grazing cessation and developing tourism (e.g. Dullinger et al., 2007; Klanderud and Birks, 2003; Michelsen et al., 2011). Thus, an effect of climate change on spread of *C. lachenalii* was more pronounced in non-grazed areas at the highest elevations, whereas in areas trampled by tourists, as well as intensively grazed in the past, signals from climate are less-pronounced and tend to be overwhelmed (Pauli et al., 2003).

The species composition of most of the lower-elevation granite grasslands without *C. lachenalii* was characterized by relatively high competition level and share of more shade-tolerant species, as well as those with

larger sizes (canopy height). This may be a consequence of upward treeline progression, induced by an impact of grazing abandonment rather than climate change (Gehrig-Fasel et al., 2007; Ameztegui et al., 2015). About 67% of the treeline length in the Tatra Mts was lowered an average for 315 m due to high historical grazing intensities (Radwańska-Paryska and Paryski, 1995). Kaczka et al. (2015) found that over the period 1949–2009, the treeline ecotone shifted upward about 35 m in the Mięguszowiecka and 11 m in the Rybi Potok valleys. This means that the treeline in the Tatra Mts did not regain its historical limit yet. We concluded that *C. lachenalii* declined on areas released from grazing pressure due to the increased inter-specific competition, and taking advantage of climate change, it colonized areas at higher elevations, characterized by high importance of habitat filtering in shaping plant communities. In tourism-disturbed plant communities it showed a tendency for horizontal spread.

4.6. Perspectives on conservation of rare mountain species

From a global perspective it seems that *C. lachenalii* is not directly endangered, but in Poland it was recorded only from a limited number of localities in the Tatra Mts. Similar range dynamics occur in other species such as *Geum reptans* – a plant occurring mostly on high-elevation granitic screes, that shows high plasticity to changing environmental conditions, e.g. increasing temperature or different competition levels (Plüss and Stöcklin, 2005). However in the future, plants that currently are not directly threatened, may become critically endangered or extinct, by factors such as dramatic increases in tourism intensity. On the other hand, the persistence of *C. lachenalii* populations on areas with high competition levels is uncertain. Therefore, to achieve the most proper form of potential future *C. lachenalii* conservation, we propose the limitation of tourist traffic, at least on areas with the highest trampling intensities, and active forms of conservation (e.g. moderate grazing) on areas with the highest competition levels, i.e. those sites where grazing was abandoned.

The interactions among species change in a warmer climate: mountain flora and vegetation become more thermophilous, dry-demanding and productive. Thus, plant specialists are replaced by generalists. Such processes are the signals of homogenization of alpine flora and vegetation (Olden et al., 2004; Britton et al., 2009; Ross et al., 2012; Evangelista et al., 2016) and are in line with the observed colonization of the highest-elevation snowbeds, indicating a potential replacement of the most specialized cold- and wet-demanding species, as well as bryophytes with low productivity, by more warm-, dry- and nitrogen-demanding *C. lachenalii*. Such replacements in the Tatra Mts presumably represent the initial stages of climate-induced succession, and are more pronounced in arctic alpine regions (e.g. Sandvik and Odland, 2014). Therefore, in our opinion the climate-induced homogenization of plant communities constitutes a serious threat to alpine flora and vegetation.

4.7. The reliability of historical records

Resurveying of botanical studies requires high reliability of historical data collection. The main issue of resampling studies is that observed compositional shifts may be affected by the incompleteness of historical data, often representing summarised reports from botanical excursions (Stöckli et al., 2011). Another factor influencing results may be resurvey efforts that are not comparable due to different and more advanced sampling techniques in comparison to those used in historical studies. However, despite these limitations, resampling of botanical studies gives unique opportunity to explore species composition changes in alpine flora and vegetation (e.g. Vittoz et al., 2008; Naaf and Wulf, 2010; Kapfer et al., 2017).

The historical distribution of *C. lachenalii* was reported by botanists well experienced in identification of the difficult genera, i.e. *Hieracium* or *Carex*, who were also good mountain climbers (Zemanek, 2012). This included the authors of previous studies on the flora and vegetation

of the Tatra Mts, e.g. Bolesław Kotula (1889–90; the distribution of vascular plants in the Tatra Mts), Bogumił Pawłowski (1956; the flora of the Tatra Mts) and Stanisław Balcerkiewicz (1984; the vegetation of the Dolina Pięciu Stawów). In addition, the specimens of *C. lachenalii* collected by these authors are deposited in the KRAM Herbarium (Kraków, Poland). Thus, we are confident, that the whole elevation gradient (including the most inaccessible areas) was surveyed carefully, and *C. lachenalii* was identified correctly. Our results were not affected by the incompleteness of historical data and higher surveying effort. The only potential uncertainty in our study was caused by missing elevations of some historical localities, and low accuracy of historical altimeters.

5. Conclusions

Shifts in distribution of *Carex lachenalii*, a model arctic-alpine species, demonstrated the main patterns of diversity changes in European alpine vegetation. The fact that habitat filtering rather than interspecific competition described *C. lachenalii* colonization on snowbeds and granite grasslands at the highest elevations may suggest that climate change, expressed by decreased snow cover duration and subsequent prolongation of growing seasons, was the main factor driving the upward shift of this plant. Moderate trampling enhanced horizontal spread of *C. lachenalii* by reducing competitors and creating new sites suitable for colonization. *C. lachenalii* declined on areas with high competition levels, i.e. those where grazing was abandoned. These three environmental factors determining shifts in distribution of *C. lachenalii* may also contribute to changes in distribution of other rare mountain plant species and should be taken into account in conservation management plans.

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